THE VELIGER


The Veliger 30(4):372–376 (April 1, 1988)

# Individual Movement Patterns of the Minute Land Snail *Punctum pygmaeum* (Draparnaud) (Pulmonata: Endodontidae)

by

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*Abstract.* Movement patterns of the minute land snail *Punctum pygmaeum* were studied in boxes provided with natural substrate. Experiments were conducted with different snail densities and box sizes, but at constant temperature and humidity. The mean displacement per 12 h averaged 47 mm and was significantly influenced by snail size, but not by box size or snail density. *Punctum pygmaeum* moved equal distances at night and during the day. Snails kept in groups showed aggregative behavior. The adaptive significance of this behavior is discussed.

## INTRODUCTION

Movement patterns, and especially distances covered, have important consequences in determining population size and genetic structure (*cf.* DOBZHANSKY & WRIGHT, 1943). Studies of individual movement patterns in terrestrial gastropods have been concerned mainly with nocturnal activity and with homing and trail following of large-sized species (*e.g., Helix pomatia* Linné [EDELSTAM & PALMER, 1950], *Euglandina rosea* (Férussac) [COOK, 1985], *Limax maximus* Linné [GELPERIN, 1974], *Limax pseudoflavus* (Evans) [COOK, 1980]). Little attention has been directed to movements of minute snail species living in leaf litter (but see BOAG, 1985). In this paper we report on individual movement patterns of *Punctum pygmaeum* (Draparnaud), the smallest among European land snails.

*Punctum pygmaeum* occurs in a wide variety of moderately moist habitats, especially in leaf litter of deciduous forests (KERNEY & CAMERON, 1979). It is one of the most abundant land snails in Europe, reaching densities of 173 snails/m$^2$ (PHILLIPSON & ABEL, 1983). However, little is known about its life history. Like other endodontoids, *P. pygmaeum* exhibits indeterminate shell growth (*cf.* SOLEM, 1976). It can reproduce in the absence of a mate (BAUR, 1987).

Several hypotheses have been proposed to explain observed movement patterns. Distances traveled have been assumed to depend on snail density (GREENWOOD, 1974; OOSTERHOFF, 1977), and they have also been found to correlate with individual shell size (*e.g., Helminthoglypta arrosa* Binney [VAN DER LAAN, 1971], *Arion ater* (Linné) [HAMILTON & WELLINGTON, 1981], *Monadenia hillebrandi mariposa* Smith [SZLAVECZ, 1986]). As a result of the mainly nocturnal activity of land snails, distances traveled at night may exceed those covered during the day (*e.g., Helix aspersa* Müller [BAILEY, 1975], *Helix lucorum* Linné [BAILEY & LAZARIDOU-DIMITRIADOU, 1986]). Our experiments were conducted to determine whether distances moved by *Punctum pygmaeum* are affected by the size of experimental containers, snail density, snail size and (or) time of day. In addition, the spatial distribution of snails was tested for deviation from randomness.

## MATERIALS AND METHODS

Specimens of *Punctum pygmaeum* were collected in an aspen (*Populus tremula*) and birch (*Betula* spp.) dominated part of the forest Nåsten 5 km SW of Uppsala in central Sweden (59°50′N, 17°40′E) in September 1986. The snails were maintained singly on decaying leaves of aspen in 50 × 10 mm petri dishes lined with moist paper towel in natural daylight at 20–22°C and 90–100% relative humidity. The size of the snails (shell breadth) was measured to the nearest 0.02 mm using a binocular microscope with a stage micrometer.

### Experimental Design

Movement patterns of *Punctum pygmaeum* on their natural substrate were recorded. For this purpose the bottom of transparent plastic boxes was lined with moist paper towel covered by a single layer of decaying leaves of aspen.

Since the movements of snails may be constrained by the size of the container, two different box sizes were used during the experiments: 12.5 × 9 × 7 cm (small box) and 24.7 × 18 × 7 cm (large box).

To test whether snail density influences movement patterns, experiments were conducted with one or four snails in each test box. To follow individual behavior, snails were marked on the shell with minute dots of correction fluid ("Tipp-Ex"). The experiments were conducted under natural light conditions at 20–22°C. Humidity in the boxes ranged between 90 and 100%. Snails were randomly assigned to different box sizes and snail densities. Each snail was tested only once, with each test trial lasting 10 days. Position recordings were made twice a day (0900 and 2100 h). Consequently, 21 positions and 20 displacements were recorded for each snail. We define movement frequency as the percent of all displacements where the snails moved 3 mm or more.

Individual movement patterns were recorded for 48 snails. Forty-one of these were collected in the field, and seven were born in the laboratory.

### Statistical Analysis

Data analysis was performed using the SAS program package (SAS Institute, Inc., 1985). A Mann-Whitney *U*-test was applied to test whether snails raised in the laboratory differed in behavior from those collected in the field. The influences of box size, snail density, time of day, and snail size on the distances covered (logarithmic transformed) were evaluated by analysis of variance (ANOVA). For this analysis snail size was divided into three size classes. The directions of successive displacements were tested for independence using $\chi^2$-test (Batschelet, 1981). The null hypothesis of this test states randomness in the directions of successive displacements. A runs-test (Sokal & Rohlf, 1969:624) was applied to test whether the snails' behavior showed periodic sequences of activity. Nearest neighbor distances were calculated for all observations to determine whether snails tested in groups of four showed aggregative behavior (Clark & Evans, 1954). These distances were compared with simulated ones (100 runs for each box size) using *t*-tests.

Simulated values, based on the assumption of random dispersion, were obtained by calculating distances between randomized snail positions.

## RESULTS

### Displacement

In terms of mean displacement and frequency of movement, snails raised in the laboratory did not differ from similar-sized ones collected in the field (Mann-Whitney *U*-test, both cases $P > 0.1$). Consequently data of both groups were pooled for further analyses.

The mean displacements of the snails are summarized in Figure 1. Since the individuals were not continuously observed, the values recorded represent minimum distances traveled over each 12-h period. Mean minimal distances averaged 47 mm with a range of 3 to 95 mm. This high variability among individuals can be explained partly by size, which significantly influenced displacement (Table 1), with larger individuals on average traveling greater distances (Figure 2). In contrast, box size, snail density, and time of day had no significant effect on mean displacement (Table 1). These results indicate that *Punctum pygmaeum* kept singly or in groups of four in each box size traveled similar distances within 12 h. However, the interaction of snail size and density was significant (Table 1).

Table 1

Analysis of variance of the minimal distance traveled by *Punctum pygmaeum* in 12 h.

| Source of variation | d.f. | SS | *F*-value | *P* |
|---|---|---|---|---|
| Model | 14 | 32.99 | 5.02 | <0.0001 |
| Error | 963 | 451.79 | | |
| Snail size (S) | 2 | 16.99 | 18.11 | <0.0001 |
| Density (D) | 1 | 0.57 | 1.21 | 0.2719 |
| Box size (B) | 1 | 0.14 | 0.31 | 0.5799 |
| Time of day (T) | 1 | 0.12 | 0.26 | 0.6122 |
| S × D | 2 | 12.73 | 13.57 | <0.0001 |
| S × B | 2 | 0.74 | 0.79 | 0.4553 |
| S × T | 2 | 0.12 | 0.13 | 0.8753 |
| B × D | 1 | 0.22 | 0.46 | 0.4986 |
| B × T | 1 | 1.33 | 2.84 | 0.0922 |
| D × T | 1 | 0.02 | 0.05 | 0.8225 |

Representative displacement tracks of two *Punctum pygmaeum* kept singly in large boxes are illustrated in Figure 3. In general, the direction of a given displacement was independent of the direction of the preceding displacement ($\chi^2$-test, all snails $P > 0.2$, but one $P < 0.01$).

### Timing of Activity

The frequencies of movement for the snails are summarized in Figure 4. Nineteen of the 48 *Punctum pygmaeum* were active during 19 or more 12-h periods, while 16 snails were active during 10–17 periods. The latter snails, however, showed active sequences of 4–6 consecutive periods interrupted by pauses of 1–3 periods (runs-test in 12 snails $P < 0.01$, in four snails $P < 0.05$). The remaining 13 snails were irregularly active with no distinct pattern.

### Aggregative Behavior

Significant aggregations of *Punctum pygmaeum* during the whole experiment were observed in three of four small boxes and in two of three large boxes (Table 2). Analysis of the snails' positions indicates that in some boxes snails rested on only a few selected leaves, while in others they

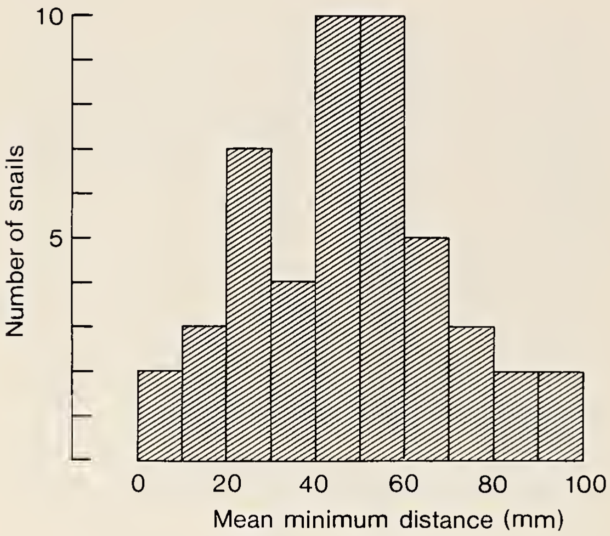


Figure 1

Distribution of mean displacements for *Punctum pygmaeum*. Each value represents the mean of 20 displacements of an individual snail during 12 h.

showed no preference for any particular leaf. Similar patterns of leaf preference were observed for boxes containing only one snail.

## DISCUSSION

### Displacement

Our results showed that individuals of *Punctum pygmaeum* moved approximately 5 cm in 12 h. However, in the course of a single 12-h period, a snail may actually travel farther than recorded here. In a pilot experiment, we monitored the actual tracks of individual *Punctum pygmaeum* creeping on wet paper towels. Stressed by the artificial light of a 40-W bulb, individual snails moved between 282 and 480 mm within 40 min (mean for 16 individuals = 407 mm), which corresponded to 6–66% of their resultant displacement (mean = 29%). Thus, one may assume that the average distance traveled is about three times the minimum displacement distance recorded here. On the other hand, the natural habitat of *Punctum pygmaeum* consists of a multiple layer of leaves and, consequently, distances traveled may result in shorter horizontal displacements. Distances covered may also be influenced by microclimatic factors. In our experiments the snails were kept under constant temperature and humidity, as seldom prevail in the field. Undoubtedly, heterogeneity in microclimate and substrate will influence snail movements under natural conditions.

The positive correlation found between shell size and distance traveled in *Punctum pygmaeum* is paralleled in other snail species (*e.g., Helminthoglypta arrosa* [VAN DER LAAN, 1971], *Arion ater* [HAMILTON & WELLINGTON, 1981], *Monadenia hillebrandi mariposa* [SZLAVECZ, 1986]). However, it seems not to be a general feature of terrestrial gastropods. For instance, no difference in distances covered between adults and half-grown juveniles was observed in *Cerion bendalli* (WOODRUFF & GOULD, 1980), *Ariolimax columbianus* (Gould) (HAMILTON & WELLINGTON, 1981) and *Arianta arbustorum* (Linné) (BAUR, 1984, 1986). In addition to size effects, the high variability in terms of distances traveled in *Punctum pygmaeum* may result from physiological and (or) genetic differences between individuals. Similar individual variation in mobility has been described for *Helix pomatia* Linné (LOMNICKI, 1969) and *Arianta arbustorum* (BAUR & GOSTELI, 1986).

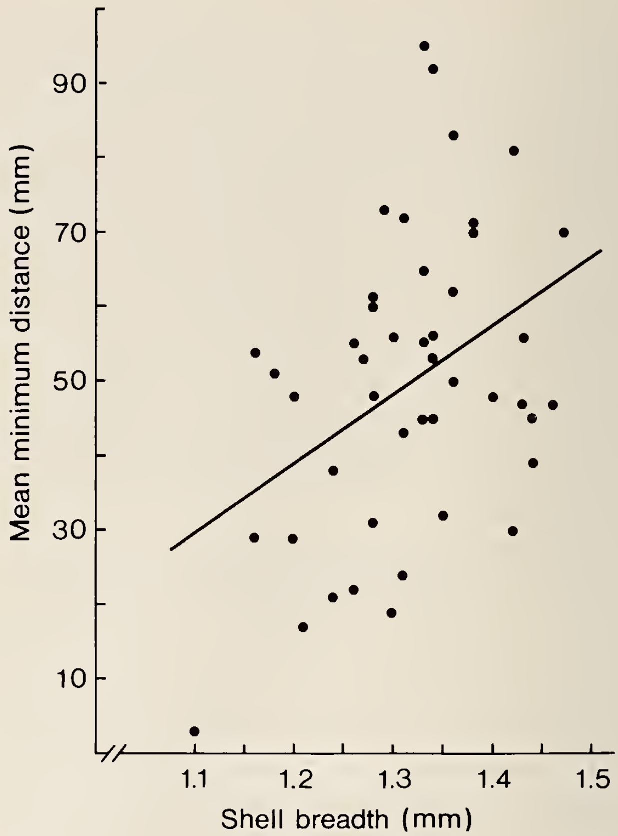


Figure 2

Relationship between mean displacement ($y$) and shell size ($x$) of *Punctum pygmaeum* ($y = 92.4x - 71.7$; $r = 0.49$, $n = 45$, $P < 0.01$).

In our experiments *Punctum pygmaeum* was kept at densities ranging from 22 snails/m$^2$ (one snail in a large box) to 356 snails/m$^2$ (four snails in a small box), while the actual density of the original population was estimated at 63 ± 38 snails/m$^2$ (mean ± SE) in September 1985 (unpublished results). However, we failed to find any influence of snail density on displacements. In the literature both density-dependent dispersal (*e.g., Cepaea nemoralis* (Linné) [GREENWOOD, 1974; OOSTERHOFF, 1977], *Arion ater* [HAMILTON & WELLINGTON, 1981]) and density-in-

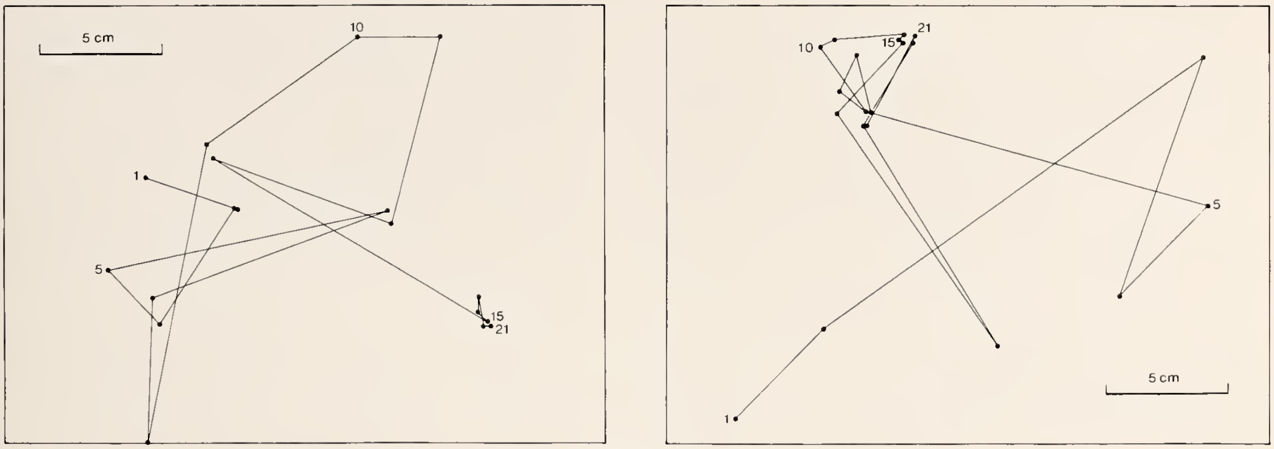


Figure 3

Representative displacement tracks of two individuals of *Punctum pygmaeum* kept singly in large boxes during 21 periods of 12 h. Numbers indicate the sequence of the snails' positions.

dependent dispersal (*e.g., Ariolimax columbianus* [Hamilton & Wellington, 1981]) have been claimed to occur.

### Timing of Activity

In contrast to other studies of gastropods (Bailey, 1975; Bailey & Lazaridou-Dimitriadou, 1986; Rollo, 1982; Wareing & Bailey, 1985), no distinct differences in activity between day and night were found in *Punctum pygmaeum*. In *Helix aspersa,* for example, 76–92% of the total activity was observed to take place during the night, with daytime activity being confined to periods of rainfall (Bailey, 1975). The apparent lack of a circadian rhythm observed in *Punctum pygmaeum* can be an artifact of the experimental set-up (natural daylight, but constant temperature and humidity), or a trait characteristic of snails inhabiting leaf litter. The latter suggestion is supported by findings of Boag (1985), who described humidity as the major factor influencing activity of the litter-dwelling snails *Discus cronkhitei* (Newcomb), *Euconulus fulvus* (Müller), *Vertigo gouldi* (Binney), and *Vertigo modesta* (Say), while light conditions *per se* appeared to play a minor role. Furthermore, snails with distinctly nocturnal activity and diurnal inactivity, such as *Achatina fulica* (Linné), have been shown to retain a circadian rhythm even when kept under constant high humidity in the laboratory (Chase *et al.*, 1980).

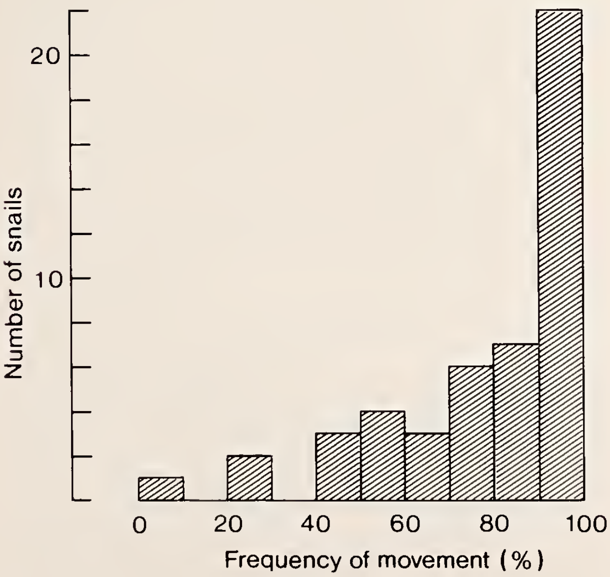


Figure 4

Distribution of movement frequencies for *Punctum pygmaeum*.

Table 2

Aggregative behavior of *Punctum pygmaeum*. The snails' dispersion is clumped if the observed nearest neighbor distances are significantly smaller than the simulated nearest neighbor distances (based on randomized snail positions). Distances are given in mm.

| Experiment | Observed nearest neighbor distance | | Simulated nearest neighbor distance | | | |
|---|---|---|---|---|---|---|
| | Mean | (SD) | Mean | (SD) | *t*-value | *P* |
| Small boxes: | | | | | | |
| I | 26.6 | (10.2) | 35.4 | (10.9) | 3.44 | <0.001 |
| II | 32.3 | (11.6) | 35.4 | (10.9) | 1.25 | N.S. |
| III | 28.1 | (9.5) | 35.4 | (10.9) | 2.88 | <0.01 |
| IV | 28.4 | (8.4) | 35.4 | (10.9) | 2.82 | <0.01 |
| Large boxes: | | | | | | |
| I | 44.9 | (17.7) | 65.1 | (22.0) | 3.95 | <0.001 |
| II | 64.2 | (24.7) | 65.1 | (22.0) | 0.17 | N.S. |
| III | 48.9 | (17.3) | 65.1 | (22.0) | 3.18 | <0.01 |

N.S. = not significant.

Aggregative Behavior

*Punctum pygmaeum* tended to aggregate. This behavior might depend upon signals emanating from the animals themselves, such as pheromones in mucus trails (*cf.* CROLL, 1983). In fact, *P. pygmaeum* clustered significantly above chance level when kept in plastic boxes without environmental stimuli capable of biasing particular locations (unpublished results). However, observations that aggregations are restricted to particular leaves in some boxes and not in others, and that snails kept singly tended to rest on some leaves more often than others, point to the effect of additional environmental stimuli. Under natural conditions, local concentrations of food (leaves with a high palatability) and high moisture may attract snails. In addition, the following of mucus trails might contribute to grouping behavior.

Aggregation is known to occur in several other gastropod species, but its adaptive significance does not appear to be the same in every case. In some species aggregative behavior may be part of reproductive activities (KUPFERMANN & CAREW, 1974), while in others it may protect snails from predation and reduce net water loss by decreasing the total surface-volume ratio (CHASE *et al.*, 1980; COOK, 1981). The adaptive advantage of aggregative behavior in *Punctum pygmaeum* is unknown.

## ACKNOWLEDGMENTS

Financial support was received from the Swiss National Science Foundation and the Ahlstrand Foundation. We thank Heidi Dobson, Staffan Ulfstrand, and an anonymous reviewer for comments on the manuscript.

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